biology letters

Spouses age at the same rate: reply to H. Kokko, 'Human parental age difference and offspring count: a comment on Fieder *et al*.'

Fred L Bookstein, Martin Fieder and Susanne Huber

Biol. Lett. 2008 **4**, 261
doi: 10.1098/rsbl.2008.0082

biology letters

Biol. Lett. (2008) **4**, 261
doi:10.1098/rsbl.2008.0082
Published online 20 March 2008

Evolutionary biology

Invited reply

Spouses age at the same rate: reply to H. Kokko, 'Human parental age difference and offspring count: a comment on Fieder *et al.*'

Our original letter published online on 29 August 2007 (Fieder & Huber 2007) has led thus far to two comments already published, each accompanied by a rebuttal from a team including the original two authors. We turn now to a third in this series of comments to be accepted for publication by *Biology Letters*. Prof. Hanna Kokko responds here to both our original communication and one of our previous rebuttals.

The model of Kokko (2008) and our model of Fieder & Huber (2007) and Fieder *et al.* (2008) are completely incompatible in their algebra. In terms of Prof. Kokko's variables x and y, the ages of the female and the male at first mating, respectively, our model of the original letter (Fieder & Huber 2007) is parametrized in terms of $(x-y)$ and $(x-y)^2$, and that of the response to Lindqvist *et al.* (2008) in terms of those two variables along with an additional term in x (the woman's age; Fieder *et al.* 2008). In either version, our model thus has three second-order terms, x^2, xy and y^2, with coefficients in fixed ratios of $1:-2:1$. The Kokko model has no term in xy, whereas in the notation of the draft from which we are working, the corresponding three coefficients are proportional to $a_y^2:0:a_x^2$. The enforcement of that zero term for the product xy of the spousal ages embodies the assumption that 'male and female age contribute independently to pair fitness'. However, this statement misrepresents the actual facts of human behaviour; the absence of interaction it enforces goes unrepresented in the raw data for any population we have ever studied. In reality, mating couples are typically approximately matched for age at the time of first reproduction, and no model that denies the fact (i.e. that does not have second-order coefficients nearly in the ratio $1:-2:1$) can come close to suiting that circumstance. Prof. Kokko's models deny that human spouses age at the same rate. Besides this missing term in the product of the ages, there is another problem with Kokko's eqn (1) as well. Any prediction equation for net offspring count must have a term in it for the 'force of mortality', the wholly predictable decline of that count with age, and this term is typically linear, or nearly, in female age. Thus, the regression coefficients reported in Fieder & Huber (2007) are unchanged when, as reported in Fieder *et al.* (2008), an additional predictor for woman's age at first birth is added into the prediction. However, in Prof. Kokko's model the slope of lifetime reproductive success on the time of pairing, controlling for male age at that time, is proportional to $1-y/a_y$, and the addition of a linear term in y, for example, would certainly change the fitted coefficient for the quadratic term. Such a result must be inconsistent with the data we reported in Fieder & Huber (2007) as well as with the additional regressions in Fieder *et al.* (2008). That the model of Fieder & Huber (2007) did not change when the force of mortality was added in is strong testimony to the robustness of the original formulation in terms of an optimum difference. That Prof. Kokko's model would necessarily change if that term were added is equally strong testimony that her model is unrealistic as applied to historical data from human populations, the subject of all the earlier letters in this thread.

In summary, while a model by which 'male and female age contribute independently to pair fitness' may conceivably apply to the leks studied in Kokko *et al.* (2006), it apparently does not apply to the human societies we and the other commentators are studying, for whom the 'optimal mate choice' is a matter of the mates who are available at any given date in a context of customs and tradition. The assumption of independent contributions of male and female age to pair fitness is clearly unhelpful in a world of strongly, and structurally, correlated mate ages, and is also incompatible with the established knowledge about the force of mortality.

Fred L. Bookstein[1,*],
Martin Fieder[1] and Susanne Huber[2]
[1]*Department of Anthropology, University of Vienna, 1090 Vienna, Austria*
[2]*Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, 1160 Vienna, Austria*
**fred.bookstein@univie.ac.at*

The accompanying comment can be viewed on page 259 or at http://dx.doi.org/doi:10.1098/rsbl.2007.0619.

Fieder, M. & Huber, S. 2007 Parental age difference and offspring count in humans. *Biol. Lett.* **3**, 689–691. (doi:10.1098/rsbl.2007.0324)

Fieder, M., Huber, S. & Bookstein, F. L. 2008 Reply to Lindqvist *et al.* 'Does parental age difference affect offspring count in humans: comment on Fieder and Huber'. *Biol. Lett.* **4**, 80–81. (doi:10.1098/rsbl.2007.0567)

Kokko, H. 2008 Human parental age difference and offspring count: and we still do not know what men or women want. Comment on Boyko and Fieder & Huber (2007). *Biol. Lett.* **4**, 259–260. (doi:10.1098/rsbl.2007.0619)

Kokko, H., Jennions, M. D. & Brooks, R. 2006 Unifying and testing models of sexual selection. *Annu. Rev. Ecol. Evol. Syst.* **37**, 43–66. (doi:10.1146/annurev.ecolsys.37.091305.110259)

Lindqvist, E., Cesarini, D. & Wallace, B. 2008 Does parental age difference affect offspring count in humans? Comment on Fieder and Huber. *Biol. Lett.* **4**, 78–79. (doi:10.1098/rsbl.2007.0514)

Received 14 February 2008
Accepted 3 March 2008